

COURTSHIP AND MATING BEHAVIOR OF
PHROSINELLA AURIFACIES DOWNES
(DIPTERA: SARCOPHAGIDAE: MILTOGRAMMINAE)

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Abstract.—The behavior of males and females of *Phrosinella aurifacies* Downes leading to courtship and mating is described and sequenced chronologically. Both sexes leave the surrounding vegetation in the morning and congregate near aphid colonies to obtain honeydew. Male-male confrontations include facing-off, sidling clockwise or counterclockwise, back-mounting and crawling-over, and trailing and chasing (often involving many males in tandem) flights. Male-male interactions intensify as the females become more abundant. Male-female interactions include facing-off, male wing scissoring; ovipositor rubbing/licking, back-mounting, and trailing, “yo-yo” and “roller coaster” flights. The behavior resulting from the male-male contacts may serve to decrease aggression and space the males, whereas that between male and female is invariably oriented toward copulation and insemination.

The genus *Phrosinella* contains six described Nearctic species: *aldrichi* Allen, *fulvicornis* (Coquillett), *fumosa* Allen, *pilosifrons* Allen, *talpina* Reinhard and *aurifacies* Downes in America north of Mexico (Downes, in Stone et al., 1965; Downes, 1985). *P. aurifacies* is a common eastern species which has been confused with *P. fulvicornis* until recently. The bright golden pollen of the facial and frontal areas and the bright orange antennae distinguish the males of *P. aurifacies* from all other congeners. The females usually differ from those of other species in having a tan to bronze pollinose frontal vitta with the color usually spreading well out onto the fronto-orbital plate. The females of *P. aurifacies* are not always separable from those of *P. fulvicornis* (Downes, 1985).

Little is known of the ethology of *Phrosinella* spp. The adults occur on sandy or gravelly soils with sparse vegetation. Females are usually seen flying near the ground in an irregular, gyrating pattern that appears to be a search flight. They are able to find closed wasp nest entrances, at which they dig and larviposit. They may also enter “wasp-sized” holes (Allen, 1926; Evans, 1970; Peckham, 1977). Nothing has been reported of the male activity and mating behavior of members of this genus (Downes, 1983, pers. comm.).

ECOLOGY

Adults of *P. aurifacies* have several generations per year in upstate New York, based upon our rearings. They occur from mid-May through mid-October. We

observed this species at three sites near Auburn, Cayuga County, and one near Chittenango, Madison County, during 1982 and 1983. The four sites, each comprised of sand or fine gravel with sparse herbaceous vegetation, were surrounded by either cottonwoods, locusts, or willows (Auburn), or, a hardwood swamp and a red pine plantation (Chittenango).

Males left the surrounding fields in early morning to congregate in open areas beneath white sweet clover (*Melilotus alba* Desr.) and cottonwood (*Populus deltoides* Marsh.). During late May and early June 1982, rainy periods dampened male activity and delayed female emergence. On sunny days the males were active from 0830 to 1840 h, and the females from 1000 to 1630 h (EDT). Both sexes reduced their activities during midday (1200–1400 h) when sand surface temperatures exceeded 45°C. Although sand surface temperatures varied from 26° to 62°C, most fly activity occurred between 35° and 40°C. In 1983 when sand temperatures in the sun reached 61°C, flies moved to the shade of the cottonwoods where surface temperatures were only 41°C. As the temperature increased, fly activity on vegetation intensified. With decreased sunlight and temperature, the flies moved back to the sand surface.

BEHAVIOR

Male interactions (Fig. 1).—*Male emergence*: The first males emerged on 17 May 1982 and 25 May 1983. They alternated resting motionless with searching for honeydew on the sand and low vegetation. While searching on the ground, the flies walked circuitously and sinuously. On vegetation, the males searched the leaf circumference and walked up and down the stems, repeatedly licking the substrate with their mouthparts. Recently emerged males spent much time on vegetation near aphid colonies.

Sand grain manipulation: Shortly after emerging and inspecting plants nearby, the males walked down from the vegetation to the ground beneath the aphid colonies and began to manipulate sand grains, interspersed with circuitous searching on the sand surface. A searching male extended his mouthparts to the sand grain, lifted it between his foretarsi and labella, and rolled it between the brushes on his foretarsi by alternately rubbing each leg forward over the grain. He then dropped the grain and stroked his mouthparts with his foretarsal brushes 2–3 times. This process was repeated 3–8 times within a 4 cm² area. A male then flew 5–10 cm away and repeated this manipulation. One male was seen manipulating a dead aphid that lay on the sand under the colony. Older males alternated sand grain manipulation with flights onto low vegetation.

Male-male encounters: During the sand grain manipulations and searching behavior, encounters between conspecific males were commonplace, resulting in bilateral tolerance, sidling or circling, face-offs, back-mounting and crawling over, trailing and/or chasing flights. Recently emerged males allowed one another to remain nearby for many minutes. Further intermale meetings led to rotating together on the ground by both males within a 4–10 cm² area. The males aligned themselves laterally, head to tail, and sidestepped clockwise or counterclockwise for 3–10 sec. Sometimes one male circled a motionless second male. Such maneuvers might then give way to any of the other above-mentioned behaviors.

As the males became more aggregatory, they approached one another and then

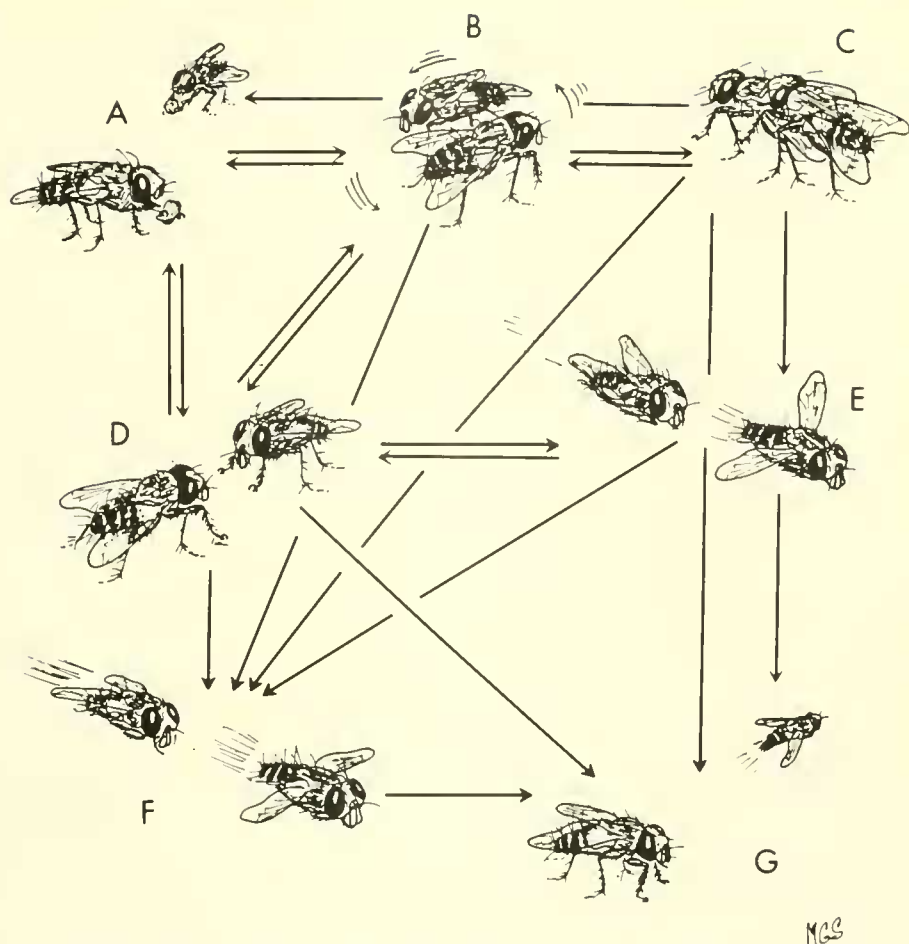


Fig. 1. Male-male encounters. A, Sand grain/vegetation manipulation (honeydew feeding). B, Sidle: two individuals walk clockwise or counterclockwise about a fixed spot. C, Back-mount/crawl-over. D, Face-off. E, Trailing flight: two or more males fly in tandem. F, Chasing flight: one male rapidly chases another. G, Separation of two males.

stood motionless face-to-face for 2–5 sec. Such face-offs may serve in sexual recognition because males had brilliant golden pollinose fronses, in contrast with tan to bronze fronses of females. Male face-offs culminated in either tolerance, feeding, back-mounting and crawling over or trailing/chasing flights. Back-mounts/crawl-overs invariably involved larger males approaching motionless smaller males from the rear, mounting them and either remaining there for 1–2 sec, or crawling over and dismounting at the opposite end.

Older males became increasingly less tolerant and chased one another in flight. This decrease in tolerance coincided with the emergence and increase in the number of females. Individual flights of males lasted 1–5 sec, attained heights of 10–30 cm for distances of 15–200 cm, and were repeated 3–16 times for a total flight time of 10–90 sec. As the fly population increased, these flights involved

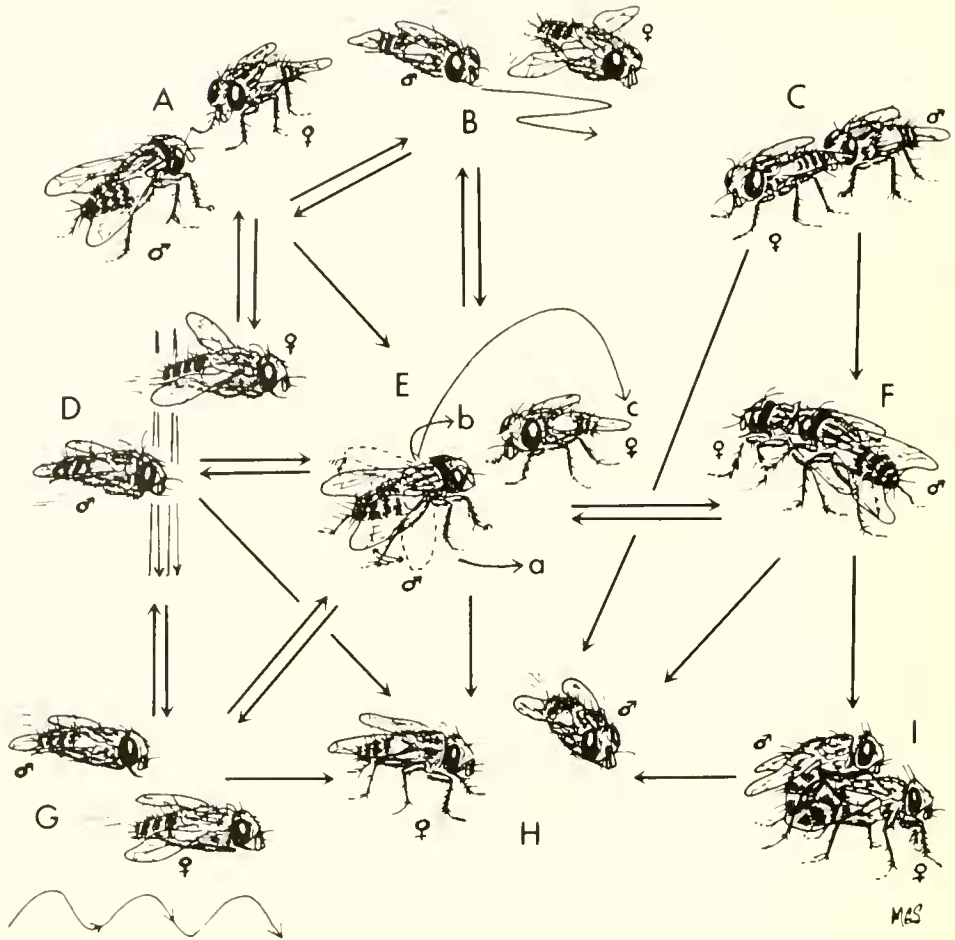


Fig. 2. Male-female encounters. A, Face-off. B, Trailing flight: male often makes zigzag flight beneath female. C, Ovipositor licking. D, Yo-yo flight: male always remains slightly below female as they both fly vertically up- and downward. E, Wing-scissoring: male scissors wings horizontally at any or all orientations (a, b, c). F, Back-mount. G, Roller coaster flight: male trails female, below her on upward portion and above her on downward portion of flight. H, Separation. I, Copulation.

as many as five males in tandem. Such flights often terminated when one or more males flew through vegetation. Some intermale encounters resulted immediately in chasing flights.

Male-female interactions (Fig. 2).—*Female emergence*: The first females of *P. aurifacies* emerged on 21 May 1982 and 6 June 1983. They walked circuitously, flew short distances, lowered their heads and paused motionless on the sand. Females focused their activities near low vegetation (*Melilotus alba*, *Taraxacum* sp., *Fragaria* sp.).

Male-female interactions involved elaborate courtship displays observed 95 times when sand surface temperatures were 26° to 49.5° (\bar{x} = 37°) C. The bisexual displays progressed from wing-scissoring (Spieth, 1974) through trailing flights, finally, to so-called “yo-yo” and/or “roller coaster” flights.

Wing-scissoring: As a male approached a female from the front the pair paused motionless on the sand in a face-off. The male then oriented his body 45° – 60° from a face-to-face alignment with hers while rapidly scissoring both wings simultaneously and horizontally for 2–5 s. During wing-scissoring a male's body sometimes waggled vigorously. A male then flew to the opposite side of a female and wing-scissored. Such bouts were repeated 3–8 ($\bar{x} = 5$) times in rapid succession, after which a male flew over and landed facing the posterior end of a female's abdomen. He either recommenced wing-scissoring, or, walked toward her and rubbed his antennae and licked with his mouthparts on her terminal abdominal segment (ovipositor?) for 1–3 ($\bar{x} = 2$) s, flew over her, landed face-to-face and repeated this sequence 1–3 times within 5–120 ($\bar{x} = 10$) s.

Some males, rather than flying over the female, sidled posteriorly across the sand, always facing her, in order to approach her from the rear. Such a male then walked toward the female and rubbed his antennae on her terminal abdominal segment. He then backed away, flew over her, landed and faced her, and recommenced his wing-scissoring.

Trailing flights: The sequence of wing-scissoring displays exhibited by a male induced a female to fly 50–250 ($\bar{x} = 75$) cm to another bare sand area, trailed 3–10 ($\bar{x} = 5$) cm by a male. Flights ($N = 42$) varied from 5–60 ($\bar{x} = 20$) cm in height and took 1–5 ($\bar{x} = 3.5$) s. Wing-scissoring by a male recommenced and the entire sequence was repeated.

"Yo-yo" flights: "Yo-yo" flights were elaborations of the trailing flights with a male trailing a female. Pairs ($N = 36$) rose repeatedly 10–40 ($\bar{x} = 25$) cm above the surface and returned to the ground from 2–9 ($\bar{x} = 4$) times in 1–6 ($\bar{x} = 2$) s, interspersed with motionless pauses of 4–20 ($\bar{x} = 6$) s or wing-scissoring. A high-pitched buzz was emitted during these and the following type of flight, but it was not ascertained which of the pair, if not both, produced the sound. Longer pauses between "yo-yo" flights occurred early in the morning (0835–0920 h) during cooler temperatures. Often, as a pair flew downward to within 5 cm of the ground, a male flew zigzag beneath a female, as though attempting to make contact with her.

"Roller coaster" flights: "Roller coaster" flights, too, were elaborations of the trailing flights, occurring usually as the sand temperatures increased. A male and female undulated in flights that ranged from 10–50 ($\bar{x} = 30$) cm above the substrate for 2–4 ($\bar{x} = 3.5$) min without landing. Sometimes during the flight the female assumed a stationary hover, 25–35 cm above the sand, for 4–7 ($\bar{x} = 6$) s, whereupon the trailing male flitted from side-to-side at 0.5–1 s intervals at a position 2–3 cm behind her. Such flights were terminated by a female landing first on the sand or leaves/twigs of nearby vegetation. A male followed and immediately commenced wing-scissoring. If he lost sight of the female when she resumed her flight, he returned to the last wing-scissoring station. The female then sallied past the male, which flew upward and followed in another "roller coaster" flight.

Many of these courtship displays terminated with either a female flying through vegetation and thereby eluding a male, the pair landing well separated, or, with the interference activities of other males. Rarely, a male lost interest in a female and flew away without any obvious external interference.

Copulation: Four copulations (1982: May 26, 1530 h, 41°C ; June 9, 1650 h, 44°C ; and 1983: June 16, 1420 and 1425 h, 41°C) began with antennal/mouthparts-

ovipositor(?) rubbing/licking, wing-scissoring, and "yo-yo"/"roller coaster" flights. Three others (1982: June 8, 1000 h, 28°C; June 10, 1020 h, 32°C; June 18, 1004 h, 29°–30°C) were observed in progress. After the "yo-yo" or "roller coaster" flights over bare sand some females flew to moderately vegetated sand, followed by a male. The male proceeded to wing-scissor vigorously, sidle to the rear of the motionless female, climb atop her and bend his abdomen under hers. Two such copulations lasted 3 and 5 min, with individual couplings of 5–90 (\bar{x} = 47.5) s. Once coupled a pair made slow, ca. 30-cm-long, flights interspersed with 5–10 s pauses, over bare sand 1–4 m away.

One pair of *P. aurifacies* on damp, shaded sand was disturbed during copulation. The male struggled for 10 s to escape the genital hold of the female, which remained motionless on the substrate during all of the male's thrashings and twistings. The male eventually flew away, after which the female continued her motionless stance. She was collected in a plastic film canister, but when the canister was opened inside of an insect net, the female made no attempt to fly upward. She was dumped into the net whereupon she remained motionless. Placed in a vial, 10 min after copulation, she still had not resumed activity, appearing to be in a state of catalepsy.

On June 18, 1982 on damp bare sand, one male mounted a female and held his body at nearly a 45° angle to her dorsum with his abdomen distinctly curved under hers. The pair remained in this position for several min during which the male held the female's wings inward and almost parallel to each other with his mid- and, sometimes, forelegs. The male's wings were held backward in a "V" position. Sometimes his forelegs rested on the dorsum of her pro- or mesothorax or atop her wings. His hindlegs grasped the substrate. All of the female's legs were on the substrate, except when she used her fore- and hindlegs for cleaning.

Eight times, at intervals of 2–8 min, the male stroked the sides of the female's wings and body with his fore- and/or midlegs, usually rubbing one side at a time. The female responded by moving her hindlegs over the edges of her wings and then rubbing the underside of her abdomen with them. Then she cleaned her face, including eyes, by moving her head in clockwise and counterclockwise directions while brushing with her forelegs. She then cleaned her mouthparts with the forelegs. The male readjusted his mount on the female four times and rhythmically moved his abdominal segments.

The pair made three flights *in copulo* that were 10, 100 and 300 cm long. Each time the pair landed on an elevated ridge and, prior to take-off and after landing, the pair assumed a horizontal rather than angular posture with the male atop the female.

After 26 min of coupling, the female kicked her hindlegs alternately for 30 s, seemingly pushing upward on the underside of the male's abdomen. The male responded by cleaning his face and mouthparts with his forelegs, then lowered himself to the horizontal position. The male disengaged, dismounted and cleaned his head and mouthparts with his forelegs. The female cleaned her head and wings, then flew a few centimeters away. She made three several centimeter-long flights, pursued by the male. The male and female then made one trailing flight; he approached her twice and attempted to mount her from the rear, but both times she sidestepped him. She then flew away, and he flew off in a different direction.

DISCUSSION

Nothing has been reported on male activity or mating behavior in the Miltogramminae. No sarcophagid, and possibly no calyptate, is known to exhibit ritualized courtship (Downes, 1984, pers. comm.). Oldroyd (1964) notes that general behavioral patterns are repetitive throughout the Diptera. Therefore, an attempt has been made to associate references based upon the described behaviors of other fly species with those observed in this study for *Phrosinella aurifacies*.

Shortly after emergence, adults of *P. aurifacies* congregate to feed upon honeydew. They spend the night in the surrounding fields and leave in the early morning where they localize beside or beneath the aphid colonies. Downes (1983, pers. comm.) has also observed this species and *Gymnoprosope milanoensis* Reinhard (Miltogramminae) feeding on honeydew. Sugar consumption by *P. aurifacies* males and females is obligatory because Miltogramminae need high concentrations of sugars to carry out their life activities (Downes, 1983, pers. comm.). *P. aurifacies* males manipulate honeydew-covered sand grains between their labella and foretarsal brushes, drop the grains, and then lap the brushes with their labella. A pheromone may be distributed by the male's foretarsal brushes. Honeydew so augmented could conceivably be used to attract conspecifics to feeding sites and thus assemble potential mates.

Because the males of *P. aurifacies* emerge first, they must wait in the area for the females. In many calyptates and, perhaps all Sarcophaginae, the males congregate at station markers (Downes, 1983, pers. comm.). In *P. aurifacies* the males await female emergence in the area near honeydew. The females emerge, feed on honeydew, mate, and then oviposit/larviposit on the appropriate hosts. Thomas (1950) found that certain sarcophagids occur regularly at specific sites. He believes that particular environmental factors, perhaps food, limit a species to a locale and thus facilitate the meeting of the sexes.

Males of *P. aurifacies*, upon emergence, congregate at honeydew sites and, as their numbers increased, male-male encounters increase. Downes (1983, pers. comm.) has also noted that an abundance of males in a small area results in much chasing activity by virtue of "chain reactions" in which a single male leaving his perch induces others to follow. The station-taking territoriality (lekking) described for Hawaiian Drosophilidae (Spieth, 1952) was not evident in *P. aurifacies*, although males became more aggressive after female emergence.

Morphological sexual dimorphism exists in *P. aurifacies*. The males possess reduced foretarsi with foretarsal brushes and brightly pollinose fronses. Many families of more primitive dipterans, e.g., Culicidae, Dolichopodidae, Sepsidae, and Drosophilidae, contain species which also exhibit sexual dimorphism (Oldroyd, 1964). Spieth (1952) states that species of Hawaiian Drosophilidae not only possess a variety of morphological dimorphisms, e.g., on the foretarsus, -tibia and -femur, but also accompanying pigmentation dimorphisms involving the mouthparts, face, antennae, wings and legs. Each male dimorphism "is involved in the male's courtship behavior" (Spieth, 1952).

No sarcophagid is known to depend on visual patterns to discriminate a mate from an unsuitable one at close range (Downes, 1983, pers. comm.), but the bright golden pollinose frons of male *P. aurifacies* appears to function as a visual cue during stationary face-offs. After a male-male face-off, the males either return to

feed, back-mount or crawl over, or one male chases the other away. After a male-female face-off, the male invariably commences courtship with wing-scissoring.

Elaborate male courtship displays are unknown for sarcophagids or calyptrates (Downes, 1983, pers. comm.), yet such precopulatory displays occur in other dipterans, e.g., mating flights in Sepsidae and Piophilidae (Oldroyd, 1964). Rau (1937) notes males and females of *Ptecticus trivittatus* Say (Stratiomyidae) hovering above garbage heaps during courtship. In addition, males of Piophilidae (Oldroyd, 1964), Drosophilidae (Brown, 1966; Spieth, 1952, 1974, 1978), and *Phrosinella fumosa* Allen (Downes, 1983, pers. comm.) circle 360° in hovering flights around a stationary female.

Wing waving is common among acalyptrates, and many males have conspicuously marked wings used to attract attention (Oldroyd, 1964). Such wing displays, which are a prerequisite to mating, may be visual and/or auditory and may involve one or both wings simultaneously, as in Drosophilidae (Brown, 1966; Bennet-Clark and Ewing, 1970; Spieth, 1952, 1974, 1978). In species where sound is the major element in mating, wing vibrations generate a species-specific sound during the wing upstroke, which the females sense with their antennal arista (Bennet-Clark and Ewing, 1970).

In *P. aurifacies*, both wings scissor simultaneously and horizontally to the substrate. Often a male of *P. aurifacies* interrupts the scissoring to rub his antennae and lick with his mouthparts on the female's terminal abdominal segment (ovipositor?). Chemicals are known to function as precopulatory stimuli in the acalyptrates, e.g., females of *Sepsis* (Sepsidae) emit an odor that can be detected by humans (Oldroyd, 1964), and males of *Drosophila melanogaster* Meigen lick a female's ovipositor for species recognition (Spieth, 1952, 1974, 1978). *P. aurifacies* males may recognize a female in this manner.

An unreceptive (immature or already mated) female *P. aurifacies* eludes a male by flying through low vegetation. On the other hand, a receptive female may initiate trailing, yo-yo, or roller coaster flights. On occasion, when a male loses sight of a female, he returns to his last wing-scissoring station, and she sallies past him, perhaps indicating her receptivity. We found no mention of such behavior for any other fly species. *Drosophila* females exhibit acceptance by wing and/or genital spreading, ovipositor extrusion, or dancing (Brown, 1966; Spieth, 1974).

Aerial capture for mating is common but not universal in the Sarcophaginae (Downes, 1983, pers. comm.) and many other Diptera (Rau, 1937; Oldroyd, 1964). Moradeshghi and Bohart (1968) state that *Euphyto* (= *Euphytomima*) *nomiivora* (James) males may either pounce directly from the air or land nearby and then jump on a female's back. Saccá (1964) states that, in *Musca*, "the union of the two sexes never takes place while flying." Similarly, in all sexual contacts by *P. aurifacies*, a male follows a female to the substrate and then climbs on her dorsum from the rear. The copulatory position assumed by *P. aurifacies* is similar to the median ventral position (Richards, 1927) of *Sarcophaga* sp. (Thomas, 1950), *Musca domestica* (Saccá, 1964), *Drosophila* spp. (Brown, 1966; Spieth, 1974, 1978), and *E. nomiivora* (Moradeshghi and Bohart, 1968).

During copulation, a male of *P. aurifacies* periodically strokes a female's wings and body with his fore- and midlegs. His foretarsal brushes may play a part in this aspect of the courtship. The female responds by rubbing her own wings and abdomen with her hindlegs. Few accounts of other copulatory behavior have been

recorded for dipterans. A *Ptecticus trivittatus* female, which assumes a position dorsal to the smaller male, caresses a male's frons and eyes with her forelegs; he responds by licking her legs with his proboscis (Rau, 1937). Moradeshaghi and Bohart (1968) make no mention of male behavior in *Euphyto nomiivora*, but state that a female intermittently stretches her legs and buzzes her wings during copulation. Males of *Musca domestica* caress a female's frons with their labella and, if she is receptive, she extrudes her ovipositor. If a *M. domestica* female is unreceptive, she kicks the male's wings with her midtibiae. *P. aurifacies* females exhibited similar behavior.

Copulation in *P. aurifacies* lasts from 3 to 26 min. Similar durations have been noted for *Euphyto nomiivora* (Moradeshaghi and Bohart, 1968). Downes (1983, pers. comm.) and Thomas (1950) state that, in Sarcophaginae, copulations last from as little as 4–5 min to over 4 h, but the shorter copulation times are atypical. According to Downes, copulations of short duration occur in species with enormous sperm pumps. He states that *Phrosinella* has one of the smallest sperm pumps in the family; therefore, the shorter copulations we observed in *P. aurifacies* may actually represent pseudocopulations (see Saccá, 1964). Moradeshaghi and Bohart (1968) report that a male of *E. nomiivora* will bend the end of his abdomen and attach it to a female's genital area to prevent successful approaches by other males. Such a pair, when disturbed, can separate immediately. Pairs *in copula* cannot be separated. Saccá (1964) states "the insemination reaction, consequent to the ejection of the spermatozoa into the vaginal sacs of *Musca domestica*, causes swelling of the latter, so at this moment the two sexes cannot part." This is probably true for *P. aurifacies* since one male was observed struggling to free himself from a female when interrupted *in copula*.

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